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Penetration of UVA into Water and its Effects on Primary Productivity with Special Reference to Water Column Mixing

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INTRODUCTION

Photoinhibition of phytoplankton photosynthesis has often been observed in surface bottles which is exposed to high light (4, 5, 6, 10, 12, 15, 16), and solar Ultraviolet A (UVA) radiation is known to be the major cause of this inhibition (2, 7). However, when algal cells are exposed continuously to UVA under laboratory conditions, acclimation of the cells to UVA was established and the photosynthetic rate recovered (8). If the acclimation occurs also in natural phytoplankton, the photosynthetic rate of surface phytoplankton would recover after several hours exposure to sunlight. This acclimation is thought to be dependent on the conditions of water column mixing. The phytoplankton may stay and be exposed to high levels of UVA at shallow depth, when the thermocline forms near the surface (17). In contrast, when the water column is mixed by wind under weak thermal stratification, the phytoplankton are transported to deeper parts of the water column where UVA is negligibly low; the phytoplankton may not become acclimatized to UVA. Therefore, inhibition and acclimatization of phytoplankton photosynthesis under natural lake conditions should be analyzed in relation to water column mixing.

The aim of the present study is to analyze the effects of stratification and water column mixing on phytoplankton photosynthesis with reference to UVA inhibition. The following experiments were performed. First, extinctions of solar UVA and photosynthetically active radiation (PAR) in water were compared with chlorophyll *a* concentrations (as phytoplankton biomass) and Secchi disk depth in lakes with various trophic conditions. Secondly, inhibition of photosynthetic rate due to UVA was measured by phytoplankton from surface and subsurface depths at a stratified lake. Diurnal changes of photosystem activity and water temperature profiles were monitored in a shallow lake. Results are discussed with reference to water column mixing, underwater light environments and acclimation of phytoplankton to UVA.

MATERIALS AND METHODS

Description of study sites and phytoplankton : Photosynthetic rates of phytoplankton were studied in Lake Nakanuma and Lake Suwa. L. Nakanuma (Ibaraki Prefecture, central Japan) is a small moderately eutrophic stratified lake where the Secchi disk depth was 1.7 m during study period. The phytoplankton composition in L. Nakanuma during the study period were mixed assemblages of different taxa, mainly cyanobacteria, centric diatoms and small green algae. L. Suwa (Nagano prefecture, central Japan) is hypereutrophic lake and dominant phytoplankton were diatoms of *Melosira* spp. during study period. The Secchi disk depth was about 1.1 m.

Measurement of Photosynthesis : Sensitivity of photosynthetic rate to UVA was compared for phytoplankton from various depths of the stratified L. Nakanuma. Water samples were collected from 0.25, 0.75, 1.5, 2.5 and 5 m using a Van Dorn sampler and placed in 2 transparent glass bottles (light : +UVA), 2 the same but wrapped with UV absorbing vinyl chloride film (light : –UVA) and 2 dark bottles (details are described in 7). Incubation was conducted at the lake surface for 2 h around noon. Oxygen concentration in the incubation bottles determined by the Azide modification of the Winkler method (1). Vertical profiles of UVA, PAR, water temperature and chlorophyll *a* concentration were measured simultaneously. Chlorophyll *a* concentration was measured fluorometrically using a fluorescence spectrophotometer (Hitachi 650–10M) after extraction with methanol (1).

Vertical variations in *in vivo* fluorescence of phytoplankton chlorophyll *a* were measured to assess the effects of water column mixing on photosynthesis at L. Suwa. Lake water samples were collected from depths of 0, 0.5, 1, 2, 3, 4 and 5 m at the lake center (maximum depth was 6 m) with an opaque Van Dorn water sampler. Samples were transferred immediately to dark bottles and stood for 1 h. Fluorescence was then measured with and without 3–(3,4–dichlorophenyl)–1,1–dimethyl (DCMU) using a Turner fluorometer which fitted with a blue excitation filter and a red emission filter. The DCMU–induced fluorescence, the difference between fluorescence with and without DCMU, was used to indicate relative photosynthetic ability in photosystem II (9). DCMU–induced fluorescence values are expressed on a common scale of relative units (not standardized by chlorophyll *a* concentration), because the temporal and vertical variations of chlorophyll *a* concentration were less than 15 % with average of 82.3 μg L^{-1}, and did not affect the diurnal changes of the fluorescence profiles.

Measurement of underwater UVA and PAR : Attenuation of UVA and PAR was measured at the following water bodies, Lake Sirakoma, Redberry Lake (Canada), Lake Tsukui, L. Biwa, L. Nakanuma, L. Suwa and 6 experimental ponds at the National Institute for Environmental Studies. Chlorophyll *a* concentration at these lakes ranged from a minimum of 0.55 in L. Sirakoma to a maximum of 144 μg L^{-1} in Senzoku Pond. Secchi disk depths measured ranged from 0.35 in Senzoku Pond and to 5.9 m in L. Biwa. The flux density of PAR in the water column was measured from 0 m to a depth of about 1% of surface density at 1 m intervals using a LI– COR quantum meter (Model 185B) with an underwater quantum sensor (SR.NO.UWQ3743, LI–COR Inc.). Underwater UVA was measured from 0 to 1.5 m at 0.1 m intervals using a UV meter (UVR–1, Topcon Co.) with a UVA sensor (UVR–36, Topcon Co.) covered with a UVA–transparent polyethylene box. Underwater extinction coefficients (k) for both UVA and PAR were calculated by the exponential model;

$$k = (\ln I_0 - \ln I_z) / z$$

where z is the depth in meters, I_0 is light intensity at the lake surface and I_z is light intensity at depth z. Extinction of UVA and PAR was analyzed with Secchi disk depth and chlorophyll *a* concentration in lake water.

To estimate the contribution of particulate and dissolved organic matter to the light extinction in water, absorbance of lake water was measured using a spectrophotometer (Shimadzu, UV–160A). Water samples were collected from the surfaces of hypereutrophic Senzoku Pond and dystrophic L. Sirakoma. Absorptions of the lake water and the lake water filtrate obtained by filtering with a glass fiber filter (GF/F) were scanned at 10 nm intervals from 200 to 800 nm. The difference in absorption between the lake water and the filtrate was considered due to particulate matter in the lake water, and that between lake water filtrate and pure freshwater (data from 14) due to dissolved organic matter.

RESULTS

UVA attenuation in lake water column : The depth to which 1 % of surface irradiance reached was 0.7 m for UVA and 1.3 m for PAR in Senzoku Pond (Figure 1a). Lake water absorbed and scattered UVA more strongly than PAR. The relationship between UVA and PAR in water, therefore, was curvilinear (Figure 1b). This implies that the ratio of UVA to PAR decreases with depth.

Extinction coefficients of UVA and PAR, which were measured at lakes with various trophic states showed positive linear correlations with chlorophyll *a* concentrations (Figure 2a). Extinction coefficients calculated for UVA were two to three times higher than those for PAR. 1 % depths of surface irradiance of UVA and PAR, which were calculated from the extinction coefficients are plotted against Secchi disk depth in Figure 2b, and both showed a positive linear correlation. The 1 % depth of PAR is about 2.4 times the Secchi disk depth. This corresponds with previous limnological findings (3). The 1 % depth of UVA is 0.7 times of the Secchi disk depth; this is the first generalization of these two parameters.

The attenuation of light in water was highly dependent on the concentration of particulate and dissolved organic matter (Figure 3). Absorption of UVA by pure freshwater is very slight. The contribution of dissolved organic matter to light absorption was greater for UV than PAR. In Senzoku Pond, UVA was absorbed and/or scattered greatly by particulate matter, i.e. mostly phytoplankton, and was absorbed slightly by dissolved organic matter (Figure 3a). In contrast, UVA was absorbed mostly by dissolved organic matter in L. Sirakoma, because the lake water contained high concentrations of dissolved humic substances and very low plankton density (Figure 3b).

Effects of light history of phytoplankton on UVA inhibition : Phytoplankton from greater depths of the stratified L. Nakanuma showed strong inhibition by UVA, while relatively weak inhibition was detected in the surface phytoplankton (Figure 4a). Because thermal stratification had been formed before and during the measurement as observed in Figure 4c, phytoplankton cells were thought to remain at each depth. Surface phytoplankton appeared to be exposed to UVA and the acclimatization would be realized (Figure 4b). In contrast, phytoplankton at greater depths would experience very low levels of UVA and would not acclimatize must be realized.

Effects of water column mixing on UVA inhibition of phytoplankton photosynthesis : Diurnal variations of temperature and photosynthetic ability which was determined as DCMU–induced fluorescence profiles were measured to analyze photosynthetic capacity with reference to water column mixing (Figure 5). At 8 a.m., water temperature was almost constant throughout the water column as it was calm and there had been no wind that morning, thus, the water column appeared to be stable. Photosynthetic ability was low at the surface and at a depth of 0.5 m, increasing and was constant below 1 m where UVA level decreased to about 1 %. Phytoplankton were considered not to acclimatize to UVA conditions because they had spent a long period in the dark. This may have been brought about the inhibition by UVA at the surface.

In the measurements at 10 a.m., 12 and 2 p.m., strong gradients of water temperature had formed near the surface due to increases in irradiance. Photosynthetic ability at each of three observations was low at the surface, and increased with depth. Photosynthetic ability of surface phytoplankton increased from 10 a.m. to 12 p.m., though surface irradiance became higher at 12 a.m. than 10 a.m.. This might have been due to the acclimatization to UVA of surface plankton which was thought to stay at the surface under stratified conditions.

At 4 p.m., a weak wind in the afternoon induced mixing of the water column. A mixing layer appeared from the surface to a depth of 1 m. Photosynthetic ability showed almost similar values in the mixing layer and higher values below a depth of 2 m. Phytoplankton in the mixing layer were thought not to be acclimatized to UVA because they did not stay at the surface. Therefore, photosynthetic ability might have shown low levels.

At 6 p.m., a stronger wind blew and caused whole water column mixing. Photosynthetic ability was constant throughout the water column. Since that time was before dawn, inhibition of photosynthetic ability by UVA was not observed.

The next morning, a strong wind enhanced the water column mixing and water temperature was almost constant throughout. Photosynthetic ability was also constant in the whole water column.

DISCUSSION

Attenuation of UVA in lakes : The depth at which UVA inhibition of photosynthetic rate is observed is variable depending on the trophic state of the lake; shallow in oligotrophic water bodies and deeper in eutrophic lakes (7). This must be due to differences of attenuation of UVA in those lakes. UVA in water measured under various trophic conditions showed that it reached greater depths in oligotrophic water bodies.

Extinction of UVA in water strongly depends on plankton biomass (chlorophyll *a* concentration). The phytoplankton density increases and the

Secchi disk depth decreases as eutrophication proceeds. The relationship between Secchi disk depth and 1 % depth of surface UVA clarified in the present study is valid in studies of the vertical profiles of phytoplankton photosynthesis with reference to high light, that is high UVA, inhibition in aquatic environments.

Dissolved organic matter in lake water, which increases as eutrophication proceeds, would also influence the attenuation of UVA because it has been shown to absorb UVA (11, 13). The contribution of dissolved organic matter to the mode of underwater UVA may be larger in humic lakes. It is thus necessary to study UVA absorption by dissolved organic matter and its effect on phytoplankton photosynthesis at various water bodies.

Effects of stratification and mixing of the water column on the UVA inhibition of photosynthesis : When considering the vertical profile of photosynthetic rate of phytoplankton in aquatic environments, mixing conditions of the water column and underwater light environment should be taken into account. Underwater light environments for phytoplankton photosynthesis are presented schematically in Figure 6. Since UVA in water is absorbed and/or scattered more strongly than PAR, UVA which penetrates through surface layer of the water column is dispersed and consequently only PAR remains in somewhat deeper layers. At greater depths, almost all PAR is also dispersed. Mixing of the water column must change the position of phytoplankton, which perform photosynthesis in variable light environments under such conditions. Figure 7 shows schematic vertical profiles of photosynthetic rate of phytoplankton with different mixing depths. When only the surface is mixed, UVA inhibition of photosynthetic rate in surface phytoplankton is small. In contrast, severe inhibition of phytoplankton photosynthetic rate at the surface is observed under deep mixing conditions, because the phytoplankton do not acclimatize to UVA due to their long stay in a layer with little UVA.

In Figure 8, 4 types of typical vertical profiles of photosynthetic ability with relation to water column mixing are presented. Type A can be observed in the morning during calm weather with no wind when mixing of the water column is not expected even under weak stratification. On such occasions photosynthetic ability is inhibited at the surface and increases with depth. Surface phytoplankton are thought not to be acclimatized to UVA, because they had spent a long night in the dark. Types B and C are both observed during the daytime. B profiles of photosynthetic ability are similar to type A, because the water column is stable under no wind and surface phytoplankton are exposed to severe UVA. When moderate wind induces the mixing of surface water (Type C), photosynthetic ability in the mixing layer is constant and increases below the mixing depth. Photosynthetic ability at the surface may vary with time of day due to the degree of acclimatization to UVA. For example, if surface phytoplankton have sufficient time to acclimatize themselves to UVA, their photosynthetic ability may increase, shown as dotted lines in types B and C. Type D might be observed on windy days. Phytoplankton show the same photosynthetic ability throughout the water column, because of intensive water mixing and insufficient acclimatization.

In conclusion, photosynthetic rate of phytoplankton in lakes is decided by degree of inhibition and acclimatization to UVA, which depends on the light history of the cells. Therefore, it is imperative to consider the surface irradiance of UVA as well as PAR, attenuation of UVA, and the mixing depth to understand the vertical profile of plankton photosynthesis in natural environments.

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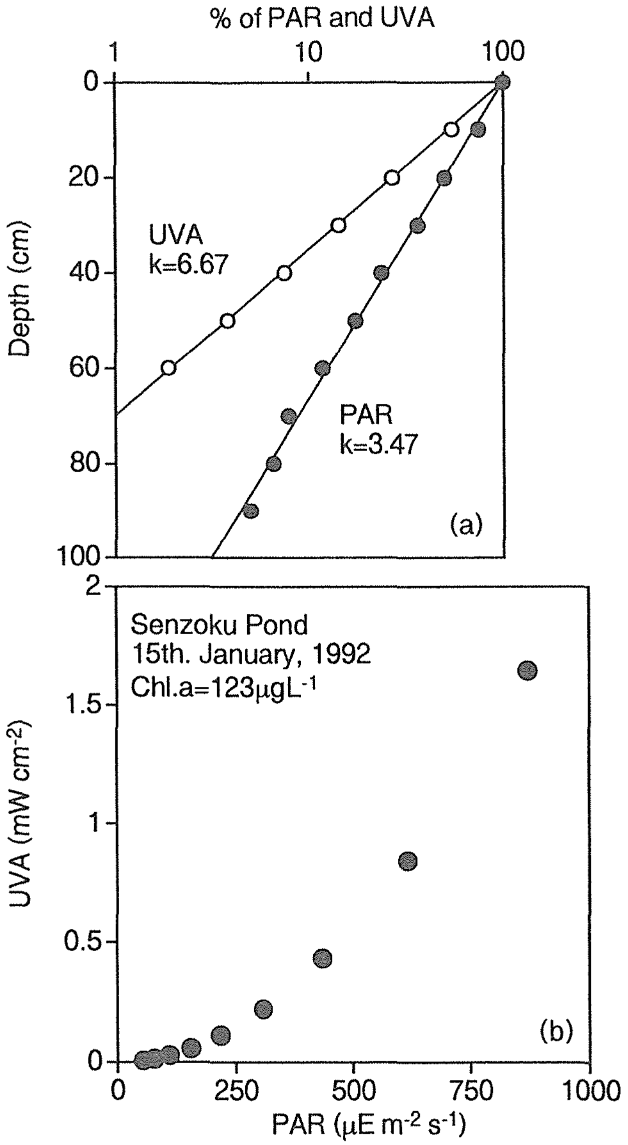

Fig. 1. (a) Underwater light penetration of PAR and UVA in Senzoku Pond. (b) Relationship between underwater UVA and PAR.

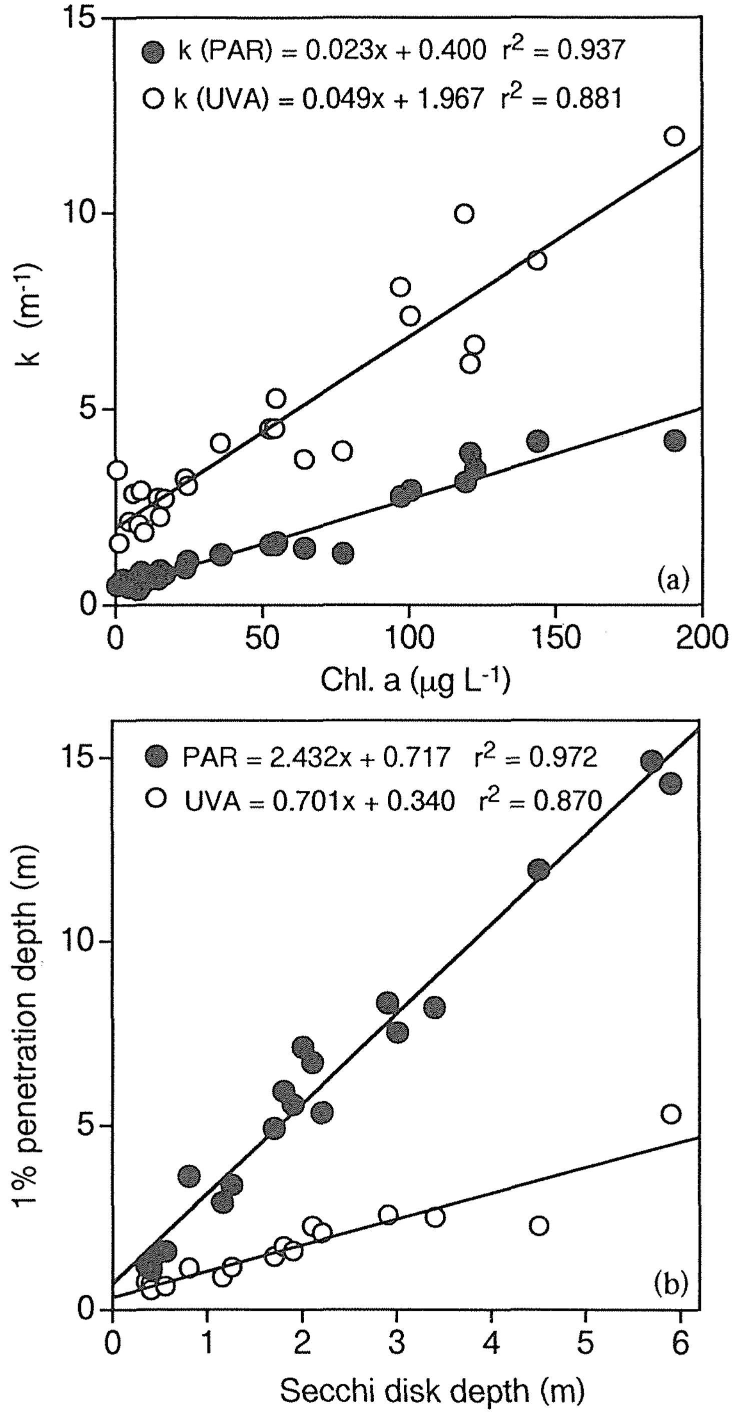

Fig. 2. (a) Light extinction coefficient (k) of PAR and UVA in relation to chlorophyll *a* concentration of the surface lake water. (b) The 1 % penetration depth of surface PAR and UVA in relation to Secchi disk depth.

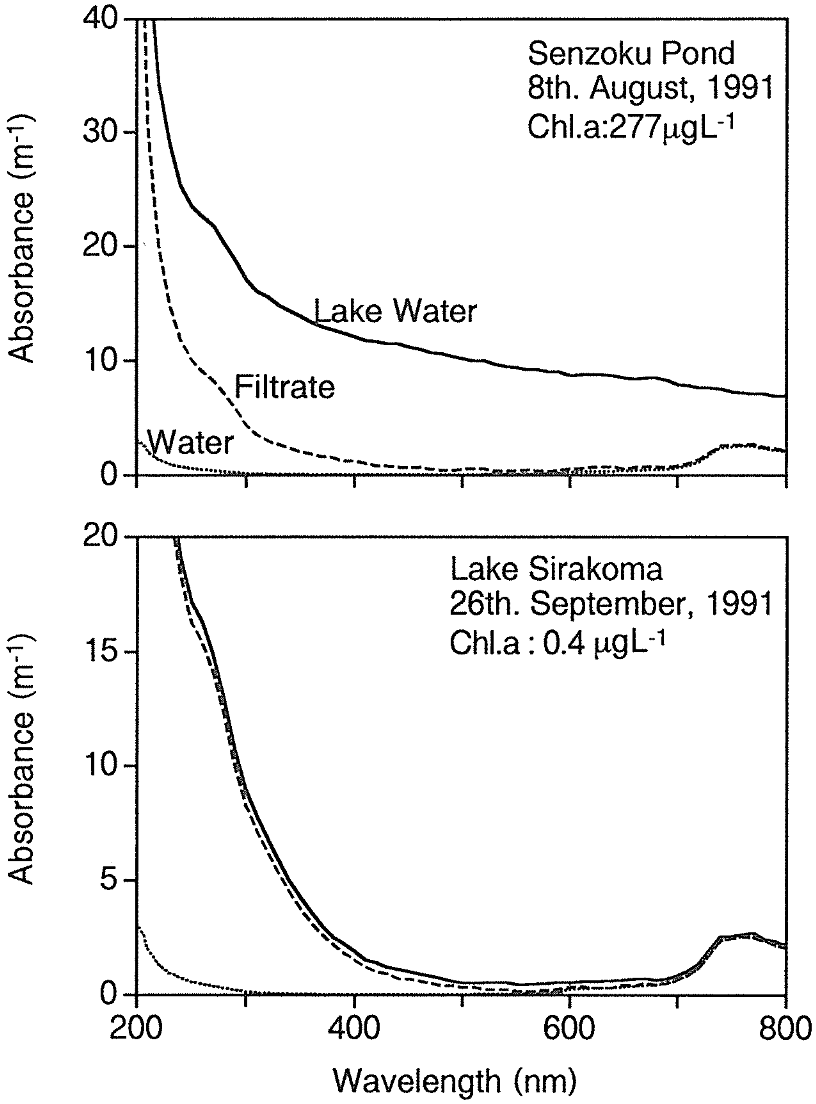

Fig. 3. Absorbance of surface samples from Senzoku Pond and Lake Sirakoma. The dotted lines are the absorbance of the pure freshwater derived from measurements in ultraoligotrophic lakes (Smith and Baker, 1981).

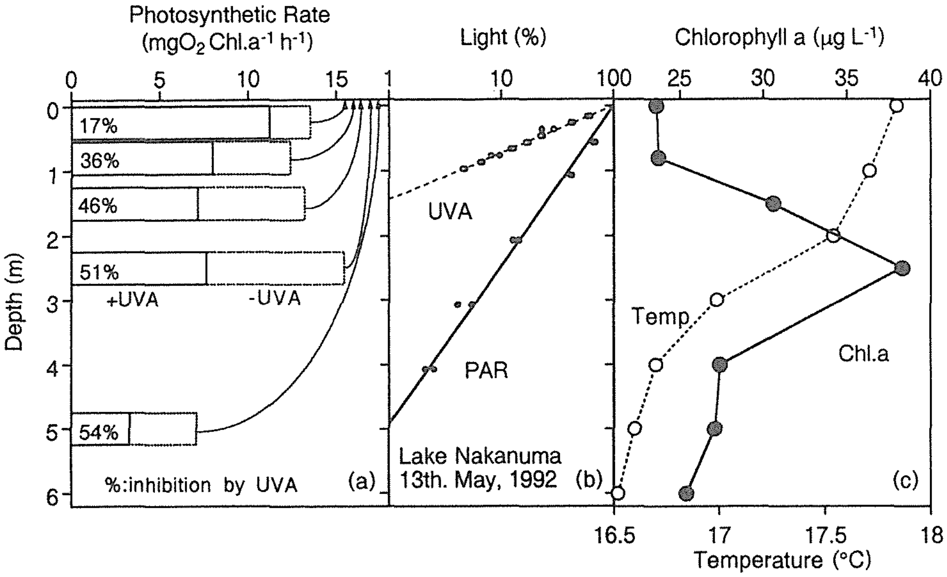

Fig. 4. Inhibition of photosynthetic rate by UVA when subsurface samples of Lake Nakanuma were incubated at the surface (a), light penetration of PAR and UVA (b) and vertical distribution of temperature and chlorophyll a concentration (c).

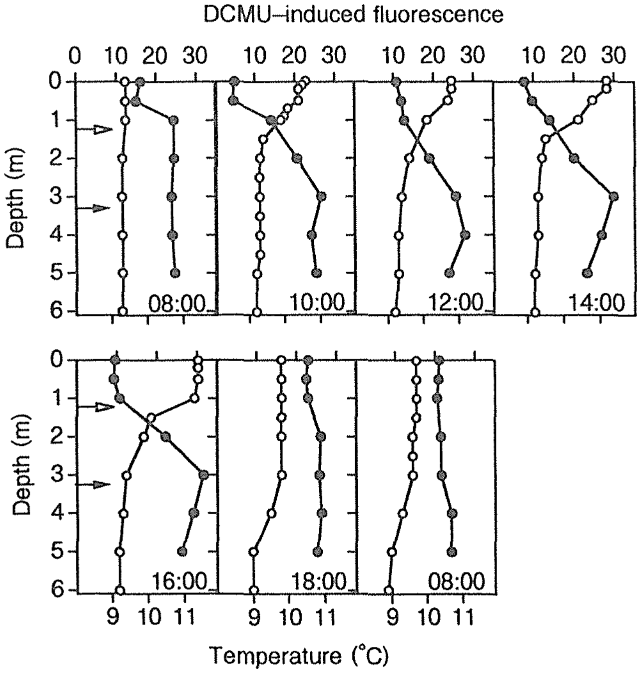

Fig. 5. Diurnal changes in water temperature (○) and DCMU–induced fluorescence of phytoplankton (●) in Lake Suwa on 17-18th. April, 1993. —▷ and —► indicate 1 % penetration depth of surface UVA and PAR, respectively.

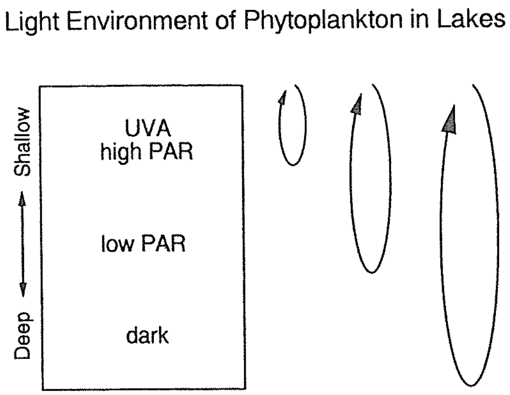

Fig. 6. Schematic model of underwater light environments for phytoplankton photosynthesis with reference to water column mixing.

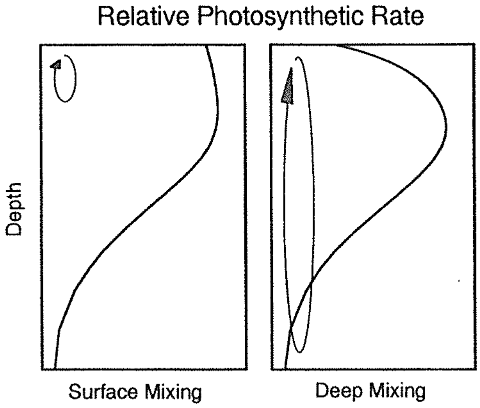

Fig. 7. Comparison of relative photosynthetic rate of phytoplankton in natural lakes with special reference to water column mixing.

Type	A	B	C	D
Wind	No	No	Moderate	Strong
Thermocline	No	Shallow	Shallow	No
Mixing	No	No	Shallow	Deep

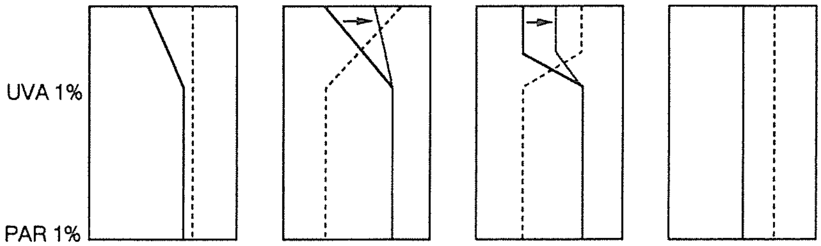

Fig. 8. Typical model of photosynthetic ability of phytoplankton (——; DCMU–induced fluorescence) with relation to water temperature (------) and wind conditions. Dotted lines (——) in types B and C indicate photosynthetic ability, when the phytoplankton acclimatize to UVA.